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Walking on trees

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For decades, standing upright and walking on the ground on two legs have been seen as defining features of the hominin clade (humans and our closest extinct relatives). However, there is increasing evidence that some Miocene apes not only had upright (orthograde) postures (1) but also incorporated bipedalism into their locomotor repertoires (2,3). Such movement may well have occurred in the trees. This raises the possibility that preadaptations for hominin bipedalism arose in arboreal settings rather than in terrestrial environments. On page xxx of this issue, Thorpe and colleagues present compelling new evidence in support of this. Using observational data from modern orangutans, they argue that hominin bipedal walking is not novel but rather a development of locomotor behaviours already established in the ancestor of great apes. In modern orangutans, hand-assisted bipedalism with extended lower limbs in the small branches of the forest canopy allows movement on slender, highly compliant supports, thus enabling them to access resources in the forest canopy that would otherwise be difficult to procure, or cross between trees with minimum energy expenditure. These advantages might well have provided sufficient selective pressure for bipedal adaptations in arboreal habitats.

One important aspect of the orangutan model is that it provides three scenarios for the emergence of modern great ape and human locomotor strategies from hand assisted, straight lower limbed, arboreal bipedalism (see Figure). In the first, forest canopy fragmentation during the Miocene of Africa led to increased vertical climbing. The authors suggest that this behaviour, which is kinematically similar to knuckle walking, predisposed gorilla and chimpanzee ancestors to the independent acquisition of forms of knuckle walking. Meanwhile in South East Asia, orangutan

ancestors became even more specialized in traversing, at canopy level, the shrinking closed-canopy forest. Finally, hominins retained and further adapted pre-existing arboreal bipedalism to exploit emerging, more open terrain between forested areas. This scenario is consistent with the long forelimbs that are found in association with obviously bipedally-adapted hindlimbs in various early hominins. It is necessary in a model such as this to simplify the nature and tempo of environmental change, although Thorpe and colleagues do point out the probable fluctuations in forest coverage that occurred during the Miocene. Inevitably, past environments were complex, and there was no straightforward transition from forested to more open habitats. Primate adaptations and radiations were equally complex, and it has been argued (4) that apes diversified into a variety of environments well before any significant Miocene forest shrinkage. Nonetheless, locomotion is strongly tied to habitat, and therefore evolves in response to external pressures, whether they are caused by environmental change or niche differentiation.

Thorpe et al.'s study reopens the debate about the origins of our own peculiar commitment to bipedal locomotion. To date, there is no consensus about the adaptive scenario that could have led to the adoption of terrestrial bipedalism. Many theories have been proposed, including the postural feeding hypothesis (5); a behavioural model (6), attributing bipedality to the social, sexual and reproductive behaviour of early hominins; the thermoregulatory hypothesis (7) which links the emergence of bipedalism to the need for thermoregulatory efficiency, and the appeasement model (8) which focuses on bipedal displays that allow for the relatively peaceful resolution of conflicts. A similar lack of agreement is also evident in discussions about the locomotor behaviour of the hominin ancestor. One possibility is that the common ancestor of humans and modern African apes used ground-based knuckle walking (9) although it has been argued that the exact nature of knuckle walking differs between African great apes (10). Other proposed locomotor modes pre-adaptive to bipedalism include arboreal quadrupedalism (11), terrestrial quadrupedalism (12,13), climbing (14) and a hylobatian model (15) which suggests a small bodied, arboreally bipedal ancestor of terrestrial bipeds.

Central to these debates is whether bipedalism arose in the trees and was taken to the ground, or whether it arose from an ancestor that was already terrestrial. The orangutan data presented by Thorpe and colleagues strongly suggest the former, and could also explain how hominin bipedality arose without needing to go through the stage of inefficient 'bent hip bent knee' bipedalism typical of modern chimpanzees. Crucially, the orangutan model also illustrates the way in which large-bodied primates could evolve straight-limbed bipedalism in arboreal contexts.

A number of fossils contemporary with the likely split of the chimpanzee/human – human clades between 4-8 Ma have been claimed to show anatomical evidence of upright posture and bipedal walking. These include *Sahelanthropus tchadensis*, *Orrorin tugenensis* and two species of *Ardipithecus*. While there is no general agreement on the locomotor and taxonomic affinities of these fossils (16), one possibility may well be that they are evidence of different ways of shifting from the ancestral type of hand-assisted arboreal bipedality proposed by Thorpe and colleagues. In later hominins, there is also evidence for locomotor diversity, within and between lineages. Limb proportions, for example, differ in *Australopithecus afarensis* and *Au. africanus* (17), and there is a range of foot morphologies in hominins from around the same time period (18). Thus, bipedal walking might have evolved independently in various early hominins. This could have occurred if multiple lineages originated from an earlier arboreal ancestor that used hand-assisted bipedalism. If that was the case, can anatomical evidence for bipedalism really be used as a crucial defining feature of hominins?

With the orangutan model, Thorpe and colleagues present a plausible and elegant argument in favour of the emergence of bipedalism in an arboreal rather than terrestrial context. In doing so, they have reinvigorated the debate over the emergence of behaviours preadaptive to bipedalism, and have shifted the focus back into the Miocene. A prediction of their model is that diversity of locomotor behaviours, including bipedalism and knuckle walking, could have arisen among descendants of an arboreally bipedal large ape. We must now question whether morphologies that indicate bipedalism can be used to identify hominins at the base of

their radiation. This then raises the issue of whether we can unequivocally identify any traits that are truly diagnostic of early hominins (19).

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